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fig. 1 pl. I

山东昌乐早始新世五图组脊齿貘类（貘超科）[1)]

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摘要 脊齿貘类是亚洲特有的中、晚始新世貘形动物，在中始新世很繁盛，但一直未发现早始新世种类。山东五图早始新世地层中发现的山东兼脊貘（*Ampholophus luensis* gen. et sp. nov.）很可能是这一类群的早期代表。它与中始新世已知种具有某些共有的特点，但仍有许多早始新世原始貘类的特征。同时，本文简单地回顾了脊齿貘类研究历史，根据现有的材料，概述了脊齿貘类的特征，根据一些进步特征将已知属分别归于脊齿貘科和红山貘科。

关键词 山东五图，早始新世，脊齿貘类

中图法分类号 Q915.877

自Matthew 和Granger 于1925 年建立脊齿貘属(*Lophialetes*)后，先后归入脊齿貘科的已有十一属。脊齿貘状原始貘形动物是亚洲始新世特有动物，在阿山头期和伊尔丁曼哈期相当繁盛，但在沙拉木仑期后很快衰落，但从未记录到早始新世标本。在山东早始新世五图组的材料中，有一上颊齿列在某些方面与脊齿貘类很相似，很可能是这类动物中唯一的早始新世代表。与这一标本共生的有 *Changlelestes*(食虫类)、*Mesodmops*(多瘤齿兽类)（童永生、王景文，1993，1994)、多种食果猴类更猴类（carpolestid plesiadapoids)（Beard and Wang, 1995)、啮齿类、古乏齿兽类和始祖貘状的貘形动物(*Homogalax*－like tapiroid)等哺乳动物化石。

由于脊齿貘状原始貘类在分类上分歧较大，对此，本文做一简单的回顾和评述。

一、化石记述

奇蹄目 Perissodactyla Owen, 1848

貘超科 Tapiroidea Gill, 1872

脊齿貘科? ?Lophialestidae Matthew and Granger, 1925

山东兼脊貘 *Ampholophus luensis* gen. et sp. nov.

（图1；图版I）

正型标本 一保存了P2－M1和M2前缘的右上颌骨（中国科学院古脊椎动物与古

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人类研究所标本登记号 IVPP V10702)。

地点和层位 山东昌乐县五图煤矿；早始新世五图组。

特征 颊齿低冠，丘－脊形齿，但齿尖清楚。上颊齿前尖、后尖等大，并明显地向舌侧倾斜，舌侧齿尖向唇侧倾斜；前附尖较小，靠近前尖；P2后脊不完全，P3、P4后脊完全，与原脊一起形成完整的原脊－后脊环。M1后小尖明显。

种、属名来源 属名指新类群兼有始祖貘和脊齿貘的特征，这在早始新世貘类中是特有的特征；种名为产地山东省的简称——鲁。

描述 标本为一年轻个体，右上颌骨上P2－M1保存完好，M2仅存前缘部分。

P2嚼面近似三角形。前尖高大，基部向舌后方伸出一初始的原脊，与牙齿后内侧齿带一起形成宽阔、封闭的三角盆。后尖小，后脊弱，也不完全，前附尖和后附尖明显。

P3嚼面卵圆形，比P2宽得多。外脊上前尖和后尖几乎等大，两尖呈圆锥形，向内倾斜，外肋显著。原尖明显地比前尖、后尖低，但有完整的原脊和后脊，并形成如*Schlosseria*前臼齿那样的原脊－后脊环，并与外脊一起围成近于半圆形的、封闭的三角凹。原尖还向后方伸出一弱棱。原脊上原小尖相当明显，前附尖显著。前、后齿带发育，原尖舌侧基部和前尖、后尖唇侧基部齿带很弱或无。

P4形态与P3相似，但尺寸较大，原小尖明显，有清楚的后小尖，从原尖向后延伸的棱脊更强。

M1呈方形。前尖和后尖近于等大，两尖唇侧坡缓，舌侧坡陡，使前尖和后尖稍向舌侧倾斜，后尖向舌侧倾斜更加明显。次尖大小与原尖相近，但有一较明显地向后尖舌后侧延伸的弱棱。后小尖很明显，在原脊上原小尖已损坏，估计可能也较清楚。前附尖较大，与前尖之间有一U形谷相隔。齿带连续，但在次尖其部缺失。

测　量（单位：毫米）

The measurements of upper cheek teeth (in mm)

P2		P3		P4		M1	
L	W	L	W	L	W	L	W
7.86	5.50	7.90	8.44	8.62	9.76	9.52	11.20

比较 已知的早始新世貘化石种类不多，其中，始祖貘(*Homogalax*)是北美华沙溪早期(early wasatchian)常见的原始貘类，*Heptodon*则是华沙溪晚期的代表，这两个属在我国早始新世地层也有发现。近来，Gingerich (1991)根据出自始新世最早期(Sandcouleean)地层中始祖貘状的化石，建立了*Cardiolophus*。在亚洲已记述两种始祖貘：周明镇和李传夔(1965)的五图始祖貘(*H. wutuensis*)和Dashzeveg (1979)的*H. namadicus*，*Heptodon*在较晚的地层中也有零星的发现。虽然这里记述的五图标本与*Homogalax*和*Cardiolophus*比较接近，但也容易与这些原始貘类相区别。这些原始貘类其上颊齿的唇侧和舌侧齿尖相对直立，不向齿列中轴线倾斜，而新种唇侧齿尖明显地向舌侧、舌侧齿尖向唇侧倾斜；已知的原始貘类的上颊齿，尤其是前臼齿的后尖清楚地比前尖小，而兼脊貘的前

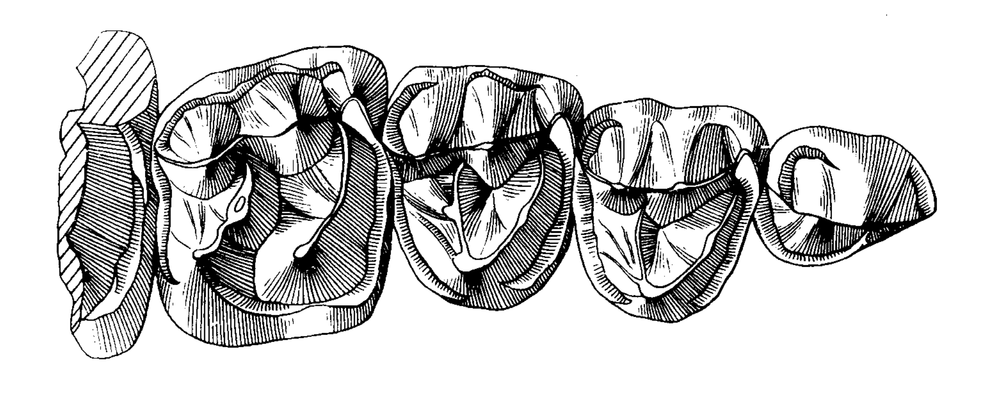


图1 山东兼脊貘，右上颊齿P2－M1(IVPP V10702)，冠面视

Fig. 1 *Ampholophus luensis* gen. et sp. nov., right P2－M1(type), occlusal view

尖和后尖几乎等大；前者的P3后脊很短，也纤弱，因而三角凹向后开放，而新种的P3后脊较强，也完全，与原脊一起形成半圆形的原脊－后脊环和封闭的三角凹；兼脊貘的原小尖和后小尖要比其他同时代的貘类相对明显；兼脊貘M1外形更近似正方形，齿冠相对低。

亚洲另一种原始貘类是丁素因(1993)记述的，产于湖南衡东早始新世早期的东方貘(*Orientolophus*)。兼脊貘与之相比，衡东种个体小，两者的第一上臼齿在形态上有明显的差异。东方貘M1的前尖、后尖虽与兼脊貘一样向舌侧倾斜，但衡东标本的后脊低弱，也较短，止于后尖的前内侧基部；而兼脊貘的M1后脊较强，几乎与原脊等高，向唇侧延伸，与前尖和后尖之间的外脊相连。东方貘前附尖很小，而在五图标本上则明显。因而，五图和衡东标本可以相区别。顺便提一下，虽然原作者怀有疑虑地将东方貘归入等外脊貘科(Isoctolophidae)，但确实如原作者指出的那样，东方貘臼齿齿尖的基本排列上与北美华沙溪最早期的始祖马(*Hyracotherium sandrae*)相似。因此，东方貘若是一种貘类的话，也是在已知貘类中在臼齿形态上最接近马形类(hippomorphs)的一个种。

*Ampholophus*在P3、P4上有由原脊和后脊形成的环形脊，这一点与亚洲中始新世繁盛的脊齿貘类相似。在脊齿貘类和与其相近的貘类中，后面两个前臼齿具有典型的环形脊是很有特点的衍生性征(Hooker, 1989)。脊齿貘亚科(Lophialestinae)、短齿貘亚科(Breviodontinae)和红山貘科(Rhodopagidae)都具这一衍征，在戴氏貘类中也具有与此相类似的前臼齿。正如上述，这一特征在早始新世貘类中只见于兼脊貘。与脊齿貘科其他成员不同，*Ampholophus*上颊齿外脊上前尖和后尖都很突出，具有明显的前尖肋和后尖肋，原尖和次尖清楚，横脊上有小尖。而在脊齿貘科的其他种属中后尖侧向收缩，前后拉长，臼齿上原尖和次尖分别与原脊和后脊融合，小尖消失，形成Radinsky(1965)所说的类似犀类的齿尖形式(arhinocerotoid－like cusp pattern)。短齿貘(*Breviodon*)上颊齿与脊齿貘科成员相似，但前臼齿数减少，只有两个前臼齿，在这一点上短齿貘

也不同于 *Ampholophus*。红山貘类分类位置有争议，红山貘类除具有类似犀类齿尖形式外，且 m3 无第三叶，与兼脊貘容易区别。早始新世的兼脊貘相对地更接近脊齿貘科的已知成员，而与红山貘类关系较疏。*Ampholophus* 和戴氏貘类一样，在后面上前臼齿都具有原脊－后脊环，但戴氏貘类的上臼齿很特化，趋于成双脊形齿。

兼脊貘的上臼齿是很有特点的，小尖清楚，唇侧齿尖外肋明显，与已知的早始新世 *Homogalax* 和 *Cardiolophus* 类似，但唇侧齿尖向舌侧倾斜，舌侧齿尖向唇侧倾斜，与之不同。这里仅据后面上前臼齿原脊－后脊环的存在，和臼齿唇、舌侧齿尖向牙齿中轴倾斜，认为五图种可能与脊齿貘类有关，并暂归入脊齿貘科。

二、讨 论

Matthew 和 Granger(1925) 记述内蒙古伊尔丁曼哈发现的 *Lophialetes expeditus* 时，建立了新亚科 —— Lophialetinae，并归入欧洲始新世的 Lophiodontidae。次年，他们又记述了阿山头期的 *Schlosseria magister*，并认为这是 *Lophialetes* 的直接祖先(Matthew and Granger, 1926)。Simpson (1945) 对这两个亚洲属的归类有疑问，没有肯定是 Lophiodontidae 或是 Helaletidae 的成员。Viret (1958) 将 *Lophialetes* 和 *Schlosseria* 归入 Helaletidae，但 Gromova (1952) 将前一属暂时放在 Lophiodontidae，却认为后者的科级分类不能确定。Radinsky (1965) 在总结亚洲早第三纪貘类化石时，将 Matthew 和 Granger 的 Lophialetinae 提高成科 —— Lophialetidae，包括 *Lophialetes*、*Schlosseria* 和 *Breviodon*，同时，也怀疑 *Rhodopagus* 和 *Pataecops*(=*Pataecus*) 也是这一科的成员。Ranga Rao(1972) 将印巴次大陆中始新世地层中发现的两个属 *Kalakotia* 和 *Aulaxolophus* 归入脊齿貘科。Birjukov (1974) 将产于哈萨克斯坦的 *Eoletes* 归入脊齿貘科，Reshetov(1975) 据一内蒙古伊尔丁曼哈的标本，建立 *Parabreviodon*，齐陶(1980) 建立了 *Simplaletes*。1988 年本文前一作者记述了山东阿山头期的 *Yimengia*，至此，已有十一属先后归入 Lophialetidae。

对这些归入脊齿貘科各个属的性质的探讨，近年来进一步展开，意见相当分歧。Reshetov (1975, 1979) 将脊齿貘科细分为三个亚科：Lophialetinae、Breviodontinae 和 Rhodopaginae。Lucas 和 Schoch (1981) 认为红山貘(*Rhodopagus*) 是一种跑犀(hyracodontid)。Hooker (1989) 使用了 Breviodontidae 和 Rhodopagidae 科名，认为 rhodopagids 是戴氏貘类(deperetellids) 的姐妹群，而 breviodontids 是脊齿貘类＋红山貘类＋戴氏貘类的姐妹群。Prothero 和 Schoch (1989a) 在奇蹄类分类中，可能据 Hooker 的意见将这些亚洲特有的貘类重新归类，设置了两个大科(magnafamily) —— Deperetellidea 和 Lophialetidea，前者包括红山貘类，后者有原脊貘科(Eoletidae Schoch, 1989) 和脊齿貘科。而 *Breviodon* 和 *Palaecops* 置于角形类(Ceratomorpha) 分类位置不确定。由此可见，目前对这些亚洲特有貘类的分类位置有不同的看法。五图早始新世兼脊貘的发现将扩大对这些亚洲特有貘类的早期历史的知识，也有利于中始新世种类分类位置的探讨。

上述亚洲特有的原始貘类绝大部分出现、繁盛于中始新世，早始新世只有本文记述的兼脊貘，中始新世之后很快衰落。印巴次大陆产 *Kalakotia* 和 *Aulaxolophus* 的地层

时代大致相当于中亚的伊尔丁曼哈期。这些原始貘类有如下共同的进步特征：上臼齿唇侧和舌侧齿尖向牙齿中轴倾斜，除 *Ampholophus* 具丘－脊形齿外，其他种类都成脊形齿，并向犀形齿发展，横脊斜伸，外脊斜向后内方；前臼齿常形成原脊－后脊环；下臼齿保留了明显的下后脊；P1 退化或缺失，如果存在，也小于门齿，紧挨 P2；上前臼齿后尖与前尖大小相近，在前尖的后方。因此，似可看作亲缘相近的一个类群，暂用 Prothero 和 Schoch(1989b) 使用的大科名—— Lophialetidea。在中亚，这些特有貘类似可分为两个亚群：一个是以 m3 具有大的下次小尖为特征，另一个的 m3 下次小尖退化或消失。前者可置于脊齿貘科 (Lophialetidae Matthew et Granger, 1925)，后者可归入红山貘科(Rhodopagidae Reshetov, 1975)。

脊齿貘科除 m3 具明显的下次小尖外，P3－4 原脊－后脊环发育；除早始新世属外，上臼齿外脊向后延长；前尖和前附尖不大向唇侧突出。根据这些特征，*Lophialetes*、*Eoletes*、*Schlosseria* 和 *Simplaletes* 可归入此科。*Breviodon* 虽 p1－2 消失，与其他脊齿貘类不同，但总体上与典型的脊齿貘类相似，似也可归入脊齿貘科。早始新世兼脊貘是相当原始的，与其他早始新世貘化石一样，上臼齿具有丘－脊形齿，小尖清楚，横脊较低，外脊不强，但其 P3－4 具原脊－后脊环和上臼齿唇侧和舌侧齿尖分别向内、外倾斜，这些特征与典型的脊齿貘类无异，因此这里也将它暂置在脊齿貘科。印巴次大陆的 *Kalakotia* 在 Hooker (1989) 的貘形亚目的分支图解中显示出与等外脊貘类 (Isectolophidae) 有某些相似点，即 p1 后无齿隙，P4 无原小尖，上臼齿原小尖和下臼齿下后附尖缺失。但这些性状在脊齿貘类中同样存在，相反，有一些特点与中亚的脊齿貘科成员一致。*Kalakotia* 上臼齿也成犀形齿，表现在后尖成扁锥状，并向舌侧位移，M3 后脊明显地比原脊短，这些特征在典型的脊齿貘类中存在，却和等外脊貘类不同。或许，*Kalakotia* 和 *Aulaxolophus* 这些印巴次大陆的特有的原始貘类，在亲缘关系上与中亚的脊齿貘类相近。

红山貘科可包括 *Yimengia*、*Rhodopagus* 和 *Pataecops* 等三属，主要的特征除 m3 缺少下次小尖外，还在于上臼齿外脊不大向后延伸，后尖更加向舌侧位移，显得前附尖和前尖格外向唇侧突出。Lucas 和 Schoch (1981) 认为红山貘是一种蹄齿犀(hyracodontid)，他们提出的与蹄齿犀类的共同点，大部分与犀形的上臼齿有关，至于 m3 无下次小尖，下臼齿横脊较高等特征在貘类中并不鲜见。在 Schoch (1989) 文章中也默认了 Hooker (1989) 的结论，即红山貘是一种貘类。阿山头期的早期红山貘类 *Yimengia* 的后面上前臼齿尚未形成典型的原脊－后脊环，而晚期的红山貘类具有原脊－后脊环。也就是说，脊齿貘科与红山貘科是平行发展的，无直接的亲缘关系，但是相当接近的两支。

鉴于上述认识，将亚洲的具有犀形齿的貘形动物分类如下：

脊齿貘大科 Lophialetidea Matthew et Granger, 1925 (Prothero and Schoch, 1989)

脊齿貘科 Lophialetidae Matthew et Granger, 1925

脊齿貘亚科 Lophialetinae Matthew et Granger, 1925

脊齿貘 *Lophialestes* Matthew et Granger, 1925

施氏貘 *Schlosseria* Matthew et Granger, 1926

始貘 *Eoletes* Birjukov, 1974

简貘 *Simplaletes* Qi, 1980
短齿貘亚科 Breviodontinae Reshetov, 1975
短齿貘 *Breviodon* Radinsky, 1965
? 脊齿貘科? Lophialetidae Matthew et Granger, 1925
兼脊貘 *Ampholophus* gen. nov.
Kalakotia Ranga Rao, 1972
Aulaxolophus Ranga Rao, 1972
红山貘科 Rhodopagidae Reshetov, 1975
红山貘 *Rhodopagus* Radinsky, 1965
奇貘 *Pataecops* Radinsky, 1966
沂蒙貘 *Yimengia* Wang, 1981

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A NEW LOPHIALETID PERISSODACTYL (MAMMALIA) FROM THE EARLY EOCENE OF WUTU BASIN, SHANDONG PROVINCE

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Key words Wutu, Shandong, Early Eocene, Lophialetid Perissodactyls

Summary

Lophialetes-like perissodactyls are endemic to central Asia, flourishing and diversifying in the Middle Eocene. Known taxa of all these tapiroids are represented in the Arshantan, Irdinmanhan, and Sharamurunian. In 1993, a specimen representing a new species was found in the Early Eocene deposits of the Wutu Basin, Shandong Province, China. This fossil may be the earliest type of the Lophialetidae. Associated with it were *Mesodmops* (Multituberculata), *Changlelestes* (Soricomorpha), *Alagomys*, *Acritoparamys* (Rodentia), carpolestid primates, and *Homogalax*-like tapiroid etc.

Perissodactyla Owen, 1848

Tapiroidea Gill, 1872

? Lophialetidae Matthew et Granger, 1925 (Radinsky, 1965)

***Ampholophus luensis* gen. et sp. nov.**

Type A fragmentary right maxilla with complete P2–M1 and anterior part of M2 (IVPP V10702).

Locality and horizon County Mine, 2km east of Wutu Village of Changle County, Shandong; Early Eocene, Wutu Formation.

Diagnosis A primitive and medium–sized tapiroid. Upper cheek teeth low–crowned and moderately lophodont, with distinct cusps; M1 metacone equal to paracone in size; parastyle relatively small, and close to paracone; labial and lingual cusps inclined to middle axis of the tooth, respectively; conules developed; P2 metaloph incomplete, P3 and P4 with continuous protoloph–metaloph loop.

Description Upper cheek teeth are unworn or slightly worn. P2 is triangular in outline, with metacone small relative to the paracone. Protoloph is low, but extends from lingual base of the paracone to lingual cingulum. Metaloph is weak. Parastyle and metastyle are clear, but not enlarged. The lingual and posterior cingula are developed, and, together with protoloph, form a closed trigon basin.

P3 is much wider than P2, and is elliptical in outline. The metacone is equal to the paracone in size, and the two cusps are almost conical, with distinct labial ribs. The labial cusps tilt lingually. The metaloph is distinctive, and with the protoloph form a successive loop, that is similar to the protoloph–metaloph loop on the posterior upper premolars of *Schlosseria*. Protoconule is clear, and parastyle distinct. Anterior and posterior cingula are developed.

P4 is similar to P3 in general, but it is larger, and has a more distinct protoconule and metaconule.

M1 is comparable to *Homogalax* in cusp pattern, with distinct main cusps. It has a more developed metaconule and protoconule than does *Homogalax*. The labial cusps, paracone and metacone, are lingually inclined, and the lingual cusps, protocone and hypocone, are labially tilted.

Comparison and discussion The new specimen is extraordinary. The upper cheek teeth consist of *Homogalax*–like molars and *Schlosseria*–like premolars. M1 of the Wutu specimen is the closest to that of *Homogalax*, among the know nearly tapiroids, in having conical main cusps, clear conules, and relatively weak ectoloph, but it is different from the known genus in some details. For example, the labial and lingual cusps converge to the mid–axis of the tooth, a characteristic also seen on the upper molars of the known *Schlosseria* and its allies. The new genus, therefore, seems to be related to the lophialetids, which are common primitive tapiroids in M. Eocene of Asia.

Matthew and Granger (1925) erected a new subfamily, Lophialetinae, for *Lophialetes*,

and allocated the subfamily into the Lophiodontidae. Radinsky (1965) raised the subfamily to the family level, including *Lophialetes*, *Schlosseria*, and *Breviodon*, and possibly *Rhodopagus*, and *Pataecops*. Some genera have been ascribed to the family since then: *Kalakotia* Ranga Rao, 1972, *Aulaxolophus* Ranga Rao, 1972. *Eoletes* Birjukov, 1974, *Parabreviodon* Reshetov, 1975, and *Simplaletes* Qi, 1980. The new species from the Wutu Formation is also referred to the family.

These tapiroids endemic to central Asia share some characters: upper molars with a rhinocerotoid-like cusp pattern, protoloph and metaloph oblique, and labial and lingual cusps converging to mid-axis; lower molar hypolophid and paralophid relatively high, and distinct metalophid; premolars non-molariform, paracone and metacone of upper premolars equal in size, the last two upper premolars with complete protoloph-metaloph loop, P1 usually absent or reduced, if P1 present, it smaller than incisors, post-P1 diastema absent. In dental morphology these central Asiatic genera can be classified into two families: Lophialetidae and Rhodopagidae.

Eoletes, *Simplaletes*, *Schlosseria*, and *Lophialetes* possibly form a monophyletic group (Hooker, 1989; Tong, 1984); and *Breviodon* (*Parabreviodon*) can considered to be their sister-group. It is obvious that the Wutu specimen is related to these Asiatic later Eocene endemic tapiroids. The new genus, like the known lophialetids, has a metaloph-protoloph loop on P3 and P4, with the labial and lingual cusps, respectively, converging to the mid-axis of M1, although it retains many primitive features. These genera constitute the family Lophialetidae, which is characterized by a large hypoconulid of m3, typical protoloph-metaloph loop of P3-4, and more elongated ectoloph of upper molars (in advanced taxa).

Kalakotia and *Aulaxolophus* from the M. Eocene of south Asia, perhaps, are equivalent to the Irdinmanhan of central Asia in age. Ranga Rao (1972) placed them in the Lophialetidae. Based on Hooker's character analysis, the Indian genera share some characters with isectolophids, and were removed from the Lophialetidae (Schoch, 1989). The traits of south Asiatic species, such as post P1 diastema lost, P4 protoconule missing and upper molar protoconule and lower molar metastylid absent, as pointed out by Hooker, are also present in the lophialetids of central Asia. Meanwhile, the presence of rhinocerotoid-like upper molars in the Indian genera suggests a close relationship with lophialetids of central Asia.

The family Rhodopagidae consists of *Rhodopagus*, *Pataecops* and *Yimengia*. *Rhodopagus* and *Pataecops* were suggested to be hyracodontid rhinocerotoids (Lucas and Schoch, 1981; Prothero *et al.*, 1986; Wang, 1988), but Prothero and Schoch (1989) agreed with Hooker's classification on perissodactyls in which the family was placed into the Magnafamily Deperetellidea. But it is true that *Rhodopagus* and *Pataecops* are closer to *Lophialetes* than hyracodontids and deperetellids. The m3 hypoconulid is also absent in tapiroids such

as *Dilophodon*. They are, therefore, thought as a sister-group of the lophialetids. The Arshantan *Yimengia* described by Wang (1988) is similar to *Rhodopagus* and *Pataecops* in dental pattern, but is more primitive than other *Rhogopagus*-like tapiroids. *Yimengia* has incipient metalophs on P3 and P4, not forming a typical protoloph-metaloph loop, as in *Rhodopagus* and lophialetids. It suggests that the protoloph-metaloph loop of the upper premolars in rhodopagids was acquired independently. But the presence of a rhinocerotoid-like molars in rhodopagids expresses a certain relationship of rhodopagids and lophialetids.

These *Lophialetes*-like tapiroids are classified as a magnafamily, including two families, Lophialetidae and Rhodopagidae.

图版 I 说明 (Explanations of plate I)

山东兼脊貘 *Ampholophus luensis* gen. et sp. nov. V10702, ×3

1. 带有 P2-M1 的右上颌骨，嚼面观 Occlusal View

2. 唇面观 Lateral View


1
2